

Chin Morphology and Sexual Dimorphism in the Fossil Hominid Mandible Sample From Klasies River Mouth

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ABSTRACT The site of Klasies River Mouth (KRM) in South Africa has produced a small sample of early Upper Pleistocene hominid remains that have been a focus for discussions of the origins of modern humans. Despite certain primitive characteristics exhibited by these fossils, proponents of a single recent origin have attributed them to early modern humans. Critics of this hypothesis have emphasized the significance of the archaic features evident in this sample, including the absence of pronounced chins among the mandibular specimens.

This study compares the size range and chin morphology exhibited by the KRM mandibles with that of Neandertals, Upper Pleistocene humans, and recent humans. The extreme sexual dimorphism documented among the KRM fossils reflects the presence of a very small individual, and previous efforts to classify the KRM sample as archaic on the basis of their robusticity have failed to address the significance of this diminutive hominid. While each KRM fossil falls within the 95% envelope of variability established for chin development in a comparative modern sample, a similarly low frequency of pronounced chins is very unlikely to be found in any recent human population. The morphological pattern of the KRM mandibles is clearly distinct from that of Neandertals and of recent humans. © 1996 Wiley-Liss, Inc.

As one of few hominid-bearing sites reliably dated to the early Upper Pleistocene, the South African site of Klasies River Mouth (KRM) has played a central role in the debate concerning the origin of modern humans. During archaeological excavations in 1967 and 1968 (Singer and Wymer, 1982), a number of hominid fossils were recovered in association with Middle Stone Age artifacts in the SAS member, which has been dated to oxygen isotope stage 5c (Deacon and Geleijnse, 1988; Deacon and Shuurman, 1992). Recent excavations have uncovered hominid fossils from the underlying LBS member, which was deposited during stages 5e and 5d (Bräuer et al., 1992). While preliminary analyses of these more ancient speci-

mens have indicated that they are metrically more similar to modern humans than to archaic *Homo sapiens* (Bräuer et al., 1992), their comminuted nature renders any taxonomic attribution equivocal. Attention remains focused on the similarly fragmented but more abundant SAS specimens, which represent the largest sample of Last Interglacial hominids from Africa. While the base of the SAS member was deposited approximately 100,000 years ago, a number of fossils

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from this layer—such as the mandibular fragments KRM 13400 and KRM 16424—likely fall between 60,000 and 85,000 years in age, while others including mandible KRM 41815 are probably as old as 90,000 years (Grün and Stringer, 1991). More securely dated than the hominid material from Omo and Border Cave (Frayner et al., 1993), the KRM sample is roughly contemporaneous with the early modern human skeletons recovered from the southwest Asian sites of Skhul and Qafzeh (Stringer et al., 1989; Valladas et al., 1988).

The hominid specimens from the SAS member have been generally accepted as anatomically modern by proponents of the single recent origin hypothesis (Bräuer, 1992; Lahr and Foley, 1994; Rightmire and Deacon, 1991; Stringer and Andrews, 1988). The identification of modern humans of such antiquity in Africa provides strong corroboration for this hypothesis, but even its supporters have acknowledged the presence of certain primitive features in this fossil sample (e.g., Stringer and Bräuer, 1994), including the extreme degree of sexual dimorphism displayed by the mandibular specimens (Rightmire and Deacon, 1991). Advocates of multiregional continuity have argued that the KRM fossils retain distinct archaic features, specifically, “very large facial remains, marked superciliary development and broad innerorbital distance, [and] the common absence of a mental eminence” (Wolpoff, 1992:46).

The first attribute cited by Wolpoff refers to the zygomatic fragment KRM 16651, the horizontal height of which was demonstrated to significantly exceed the size range observed within a sample of Holocene Cape Africans and Asian Indians (Smith, 1993), two groups that are characterized by small faces among extant human populations (Howells, 1989). Stringer and Bräuer (1994) questioned the validity of this measurement while noting that the fossil zygomatic falls in the size and morphological range of modern Europeans. Frayer et al. (1994) have argued that modern Cape Africans are a more appropriate comparative population for a fossil from southern Africa, but a significant post-Pleistocene decrease in craniofacial size has been well documented in many areas of

the Old World, including southern Africa (Rightmire, 1975, 1981), Europe (Frayner, 1984), south Asia (Kennedy, 1984), east Asia, and Australasia (Brown, 1993). Smith (1993) noted that KRM 16651 is larger than the zygomatics of the early Upper Pleistocene Florisbad and Ngaloba crania, and that its pillar-like frontal process is not common among recent peoples; however, in a sample of Holocene specimens from east and South Africa, Bräuer and Singer (1996) have documented zygomatics exhibiting size and morphology comparable to that of the Klasies specimen.

The second and third archaic features, observed by Wolpoff (1992) on frontal fragment KRM 16425, have not been recognized by all proponents of multiregional continuity. Smith (1993:242) stated that KRM 16425 “certainly does not exhibit the level of supra-orbital projection of earlier African specimens, including Florisbad and Ngaloba.” In order to explain this lack of supraorbital development, Frayer et al. (1993, 1994; Smith, 1992, 1993) queried whether this specimen represents a juvenile archaic individual. Given the current disagreement over its age, the taxonomic attribution of this fragmentary frontal specimen will likely remain a topic of contention.

The final attribute listed by Wolpoff—the absence of chins among the KRM mandibular sample—is the topic of this paper. As a homologous and derived trait among recent human populations (Lieberman, 1995), the presence of a chin has been considered to be phylogenetically diagnostic (Stringer et al., 1984). The enigmatic nature of this character within the KRM sample is illustrated in a comment by one of the site’s original excavators, who noted the recovery of “mandibles of *sapiens* and Neanderthal type” (Wymer, 1982:139). This reference to a hominid taxon whose range was restricted to Europe and west Asia reflects one of the major difficulties in assessing the taxonomic affinity of the KRM mandibles: the lack of a comparative African sample of adult mandibles securely dated to the Middle and early Upper Pleistocene. The five KRM specimens are illustrated in Figures 1 and 2; photographs and more detailed descriptions of these fossils have been presented elsewhere

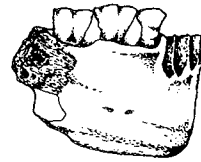
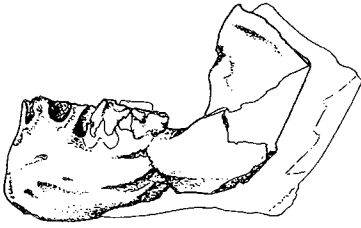


Fig. 1. Lateral views of (top) KRM 41815 and (bottom) KRM 16424.

(Rightmire and Deacon, 1991; Singer and Wymer, 1982).

This paper examines the two most commonly discussed features of the mandibular sample: the degree of sexual dimorphism and the frequency of chins. As noted by Rightmire and Deacon (1991), the extreme size range in the sample reflects the presence of the small individual represented by KRM 16424; the other four fossil mandibles belonged to distinctly larger individuals. These latter four specimens preserve at least part of the symphysis. Frayer and Wolpoff (1993) have claimed that two of these mandibles do not exhibit mental eminences; Smith (1993) has counted three specimens without this feature. Rightmire and Deacon (1991:151) offered a more generous assessment, stating that within the sample "a chin eminence is relatively prominent." At the

Fig. 2. Lateral views of (top) KRM 14695, (middle) KRM 13400, and (bottom) KRM 21776.

same time, Rightmire (1986:216; Rightmire and Deacon, 1991) observed that KRM 13400 has a nearly vertical symphyseal axis, but argued that the specimen likely fell "within the range of variation to be expected in a modern population" without specifying said range. The one mandible with an undeniable chin—KRM 41815—has been considered pathological by Frayer et al. (1993; Frayer and Wolpoff, 1993), who proposed that this pronounced morphology simply reflects alveolar resorption following pre-mortem tooth loss. Rightmire (1986) acknowledged the pathological nature of this individual but did not attribute the presence

of a chin to this condition. Smith (1992) has described the same specimen as robust but modern in form and exhibiting a distinct chin. These disparate conclusions reflect the subjectivity inherent to assessments of chin development among the limited sample of early Upper Pleistocene hominids.

MATERIALS AND METHODS

To assess the phylogenetic affinity of these KRM fossils, a comparative sample of mandibles representing Neandertals and Upper Pleistocene and recent humans was examined. This sample included sub-Saharan Africans (15 Bushmen and 15 Zulu), Melanesians (52 Tolai from Ralum, New Britain), 13 Neandertals, and nine Upper Pleistocene fossils generally accepted as anatomically modern humans. The Neandertal specimens consisted of Amud I, Tabun C1, Shanidar 2, St. Césaire, Vindija 206, Monte Circeo 3, Spy I, Montmaurin, La Ferrassie, and four mandibles from Krapina (E, G, H, and J). The Pleistocene early modern humans were represented by Border Cave 2, Border Cave 5, Fish Hoek, Matjes River, Skhul IV, Skhul V, Predmosti III, Cro-Magnon I, and Cro-Magnon II. Aside from the KRM specimens, data for fossil hominids were obtained from casts. To eliminate the possibility of interobserver variability, all measurements were taken by the first author.

Two sets of measurements were recorded for each comparative specimen. Not all measurements could be taken for all specimens, particularly in the case of the fossil casts. The first set of six measurements was chosen to assess the size range among the KRM sample and included: (1) corpus breadth at symphysis, (2) corpus height at symphysis, (3) corpus breadth at M_1 , (4) corpus height at M_1 , (5) buccolingual diameter of M_1 , and (6) buccolingual diameter of M_2 . Height and breadth were taken parallel and perpendicular, respectively, to the vertical inclination of the corpus. Molar measurements were not recorded for fossil casts. All measurements in this series were taken with digital calipers and recorded to the nearest 0.1 mm.

The second series of measurements was designed to quantify chin morphology and reduce subjectivity in assessing the presence

of this feature. According to Tillier's (1981) definition, which conforms closely to that of Weidenreich (1936), the chin is derived from two ontogenetic processes: the development of a trigonum mentale, which is composed of a central tuber symphyseos flanked by the tubercula lateralia, and the development of an incurvatio mandibulae anterior, the subalveolar depression. Enlow (1990) identifies the two processes of chin development in slightly different terms: as the deposition of bone on the mental protuberance and the resorption of the alveolar area just above it. While the chin is technically a three-dimensional feature, this study focuses on its two dimensions on the symphyseal plane.

With the mandibular specimens placed on a flat horizontal surface, a contour guide with wires approximately 0.5 mm in diameter was used to obtain the outline of the anterior border of the symphysis. The outline was taken perpendicular to the horizontal plane tangent to the base of the corpus. A line level was attached to the contour guide to ensure consistency in positioning. From a tracing of this outline, four measurements were taken (Fig. 3): (1) the angle of the line drawn from the anterior alveolar margin tangent to the basal protrusion—a general estimation of the development of the tuber symphyseos which corresponds to Measurement 79c of Bräuer (1988); (2) maximum depth of the subalveolar fossa (*incurvatio mandibulae anterior*) from this tangent line; (3) maximum anterior basal protrusion beyond the alveolar margin—another measurement of the tuber symphyseos; and (4) corpus height perpendicular to base. Angles were measured to the closest degree; the remaining measurements were recorded to the nearest 0.5 mm. Two shape indices were created by dividing measurements 2 and 3, respectively, by 4 to account for differences in mandibular height.

Identical measurements were taken for the five KRM mandibular specimens from the SAS member (KRM 13400, 14695, 16424, 21776, and 41815). Due to the fragmentary nature of the sample, not all measurements could be recorded for each specimen. Only three of the fossils (KRM 13400, 16424, and 41815) were complete enough to be used in the analysis of size. Only KRM

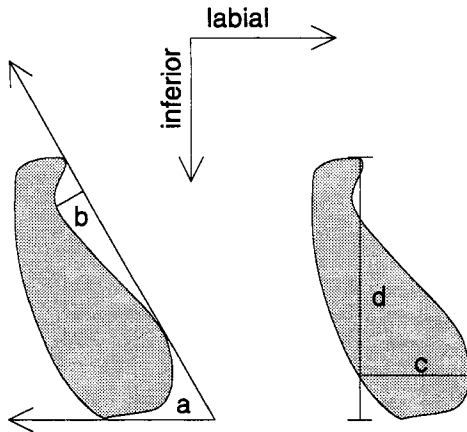


Fig. 3. Chin measurements (please see text for description).

13400, 14695, and 21776 could be used in the analysis of chin morphology; the symphyseal region was not preserved on KRM 16424 and was heavily damaged superiorly on KRM 41815. Because of some damage to KRM 14695, its corpus height at symphysis was estimated and its orientation for the morphological measurements was unavoidably subjective. The slight erosion of the alveolar margin of KRM 13400 and 21776 required the corpus height of these specimens to be estimated as well; our estimates were consistent with those provided by Rightmire and Deacon (1991).

RESULTS

Table 1 presents the means, standard deviations, ranges, and sample sizes for the KRM sample and each of the comparative groups. Not unexpectedly, corpus height at symphysis and corpus height at M_1 were highly correlated ($r = 0.746$, $P < 0.001$), as were chin angle and maximum anterior basal protrusion ($r = 0.956$, $P < 0.001$). To avoid redundancy, the former variable of each pair was not incorporated into the subsequent statistical analyses.

Figure 4 is a bivariate plot of corpus breadth vs. corpus height at M_1 comparing the KRM specimens with the recent and fossil samples. The fossils fall at the edges of the distribution, with the two larger individ-

uals at the high end and KRM 16424 near the low extreme. Figure 5, which plots M_1 breadth vs. M_2 breadth, shows the two larger fossils well within the range of the Bushman sample, with KRM 16424 as a low outlier.

A Euclidean distance analysis was run using these three KRM specimens on the basis of four variables: corpus breadth at M_1 , corpus height at M_1 , M_1 breadth, and M_2 breadth. After all possible pairwise contrasts were calculated for the modern comparative samples, it was determined that there was a less than 1 in 10,000 chance of finding in those populations a pair with an average taxonomic distance equivalent to that observed between KRM 16424 and either of the larger KRM specimens.

Bivariate plots of the subalveolar fossa index vs. the basal protrusion index compare the KRM specimens with the recent and fossil samples in Figure 6. The KRM chins cluster near the low extreme, exhibiting even less subalveolar depression than some Neandertal specimens. The Neandertal sample may be separated into two groups that coincide with their relative antiquity. The cluster to the left of the KRM sample represents the fossils from Krapina, which date to the terminal Middle Pleistocene (Rink et al., 1995); the remainder, which fall above the KRM mandibles, consist of more recent Neandertals, including Amud 1, Spy 1, La Ferrassie, St. Césaire, and Shanidar 2.

DISCUSSION

The diminutive size of KRM 16424 was recognized by Rightmire and Deacon (1991), who also noted that this specimen possessed a robusticity index similar to those of the large KRM mandibles. They focused their attention on the extreme range of sexual dimorphism that KRM 16424 established within the mandibular sample, which appeared consistent with a similar size difference observed between the two maxillary specimens from the lower LBS member (Rightmire and Deacon, 1991). A number of researchers (Armelagos and Van Gerven, 1980; Frayer and Wolpoff, 1985; Oxnard, 1987) have investigated the evolutionary trends of sexual dimorphism in the hominid lineage and, despite a paucity of fossil mate-

TABLE 1. Summary statistics¹ for KRM and comparative samples

	n	Mean	SD	Range
<u>Klasies River Mouth</u>				
Corpus breadth at symphysis	4	15.1	1.4	13.5–16.6
Corpus height at symphysis	2	32.8	0.3	32.6–33.0
Corpus breadth at M ₁	4	15.0	2.5	11.8–17.5
Corpus height at M ₁	3	28.2	6.8	20.5–33.5
Buccolingual diameter of M ₁	3	9.6	1.2	8.5–10.8
Buccolingual diameter of M ₁	3	9.7	0.8	8.8–10.2
Symphyseal angle	3	93.7	0.6	93.0–94.0
Depth of subalveolar fossa	3	0.5	0.5	0.0–1.0
Anterior basal protrusion	3	1.5	0.5	1.0–2.0
Vertical corpus height	3	27.8	5.1	22.0–31.0
<u>Bushman</u>				
Corpus breadth at symphysis	15	13.5	1.1	11.8–15.9
Corpus height at symphysis	15	29.6	3.0	24.0–35.8
Corpus breadth at M ₁	15	13.8	1.6	11.5–16.0
Corpus height at M ₁	15	25.5	2.0	23.2–29.5
Buccolingual diameter of M ₁	13	10.2	0.7	9.2–11.5
Buccolingual diameter of M ₁	13	10.1	0.5	9.5–10.8
Symphyseal angle	15	105.1	5.7	92.0–114.0
Depth of subalveolar fossa	15	1.6	0.8	0.0–2.5
Anterior basal protrusion	15	5.8	2.3	2.0–11.0
Vertical corpus height	15	28.0	4.1	20.5–36.0
<u>Zulu</u>				
Corpus breadth at symphysis	15	14.6	1.7	10.9–17.7
Corpus height at symphysis	15	33.2	3.5	25.5–39.5
Corpus breadth at M ₁	15	13.9	2.1	10.1–17.3
Corpus height at M ₁	15	29.3	3.1	24.2–36.1
Buccolingual diameter of M ₁	14	10.6	0.5	9.9–11.5
Buccolingual diameter of M ₁	15	10.2	0.7	9.1–11.4
Symphyseal angle	15	106.1	9.1	87.0–125.0
Depth of subalveolar fossa	15	2.2	0.7	1.0–3.5
Anterior basal protrusion	15	6.8	3.4	–1.5–12.0
Vertical corpus height	15	31.1	3.7	21.0–36.5
<u>Tolai</u>				
Corpus breadth at symphysis	51	15.2	1.5	11.8–18.5
Corpus height at symphysis	50	30.0	3.0	23.9–38.5
Corpus breadth at M ₁	51	14.2	1.6	10.5–17.0
Corpus height at M ₁	51	28.0	2.8	20.5–37.4
Buccolingual diameter of M ₁	50	11.3	0.5	10.1–12.4
Buccolingual diameter of M ₁	47	10.8	0.6	9.5–12.4
Symphyseal angle	48	98.5	5.7	88.0–110.0
Depth of subalveolar fossa	48	1.7	0.8	0.0–3.5
Anterior basal protrusion	48	3.1	1.9	0.0–7.0
Vertical corpus height	48	28.9	2.7	24.0–36.0
<u>Neandertal</u>				
Corpus breadth at symphysis	13	15.2	1.5	12.3–17.7
Corpus height at symphysis	13	34.8	3.7	28.0–41.0
Corpus breadth at M ₁	13	15.3	1.3	13.5–17.9
Corpus height at M ₁	13	30.5	2.4	26.3–33.5
Symphyseal angle	10	90.0	5.1	83.0–96.0
Depth of subalveolar fossa	9	1.6	1.0	0.5–2.5
Anterior basal protrusion	9	0.2	2.4	–3.0–3.5
Vertical corpus height	9	34.1	4.3	25.5–41.0
<u>Pleistocene modern</u>				
Corpus breadth at symphysis	8	15.9	2.4	12.4–20.7
Corpus height at symphysis	8	35.2	4.4	29.0–42.2
Corpus breadth at M ₁	9	13.5	2.3	11.2–17.1
Corpus height at M ₁	8	31.3	4.6	21.8–36.8
Symphyseal angle	6	106.2	9.9	95.0–121.0
Depth of subalveolar fossa	6	2.4	1.1	1.5–4.0
Anterior basal protrusion	6	6.1	3.8	2.0–12.0
Vertical corpus height	6	31.5	4.6	24.5–36.0

¹ Measurements are in millimeters, with the exception of the symphyseal angle.

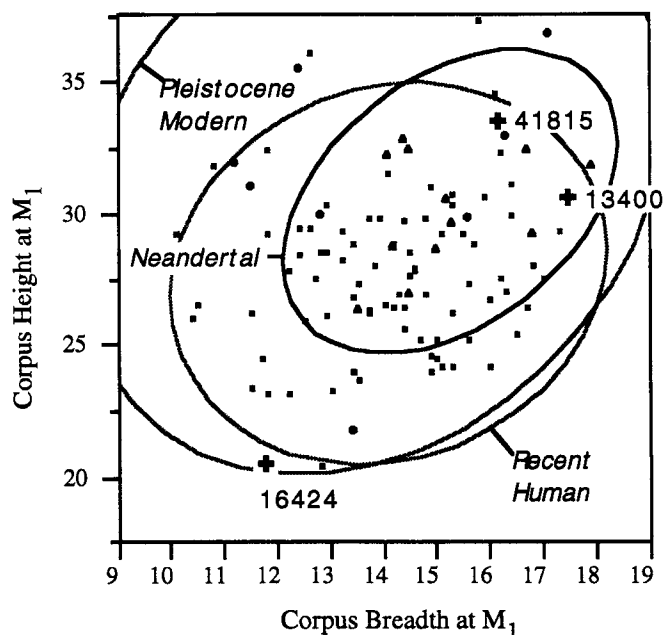


Fig. 4. Bivariate plot of corpus dimensions at M_1 (mm) for comparative samples. A density ellipse surrounds 95% of the points in each group. A "+" denotes a KRM fossil; Neandertal, Pleistocene modern, and recent human individuals are represented, respectively, by triangles, diamonds, and small squares.

rial from the Middle and early Upper Pleistocene, have concluded that this characteristic decreased through time. Frayer (1980, 1984) has documented a decrease in sexual dimorphism *within* anatomically modern humans between the Upper Paleolithic and the Neolithic of Europe; Deacon (1993) has hypothesized a similar trend for late Pleistocene humans in Africa. Similarly, Brace and Ryan (1980) found a significant difference in average tooth dimorphism between prehistoric and modern populations. The Upper Paleolithic and Mesolithic European groups in their study displayed significantly greater sexual dimorphism than the modern populations, falling completely outside the range of the larger modern samples ($n \geq 10$ per sex). Of particular relevance to this study, the percent dimorphism observed for the M_2 in the Upper Paleolithic sample falls more than two standard deviations away from each of the values for the modern populations. Substantial reduction in the degree of sexual dimorphism appears to have occurred in human populations whose modernity is not in question.

The observation of extreme sexual dimorphism in the KRM sample is based on the assumption that only KRM 16424, by far the smallest of the five mandibular fragments, represents a female. If any of the other mandibles represents a female, then the average dimorphism for this sample would be significantly less than the maximum observed dimorphism. In his study of sexual dimorphism among prehistoric Europeans, Frayer (1980) presented observed ranges for a number of measurements, including mandibular corpus height at M_2 , that provide an interesting comparative sample. Calculations of maximum dimorphism (largest observation divided by smallest observation) for this measurement produce values of 1.38 for the Upper Paleolithic sample ($n = 16$), 1.49 for the Mesolithic ($n = 45$), and 1.86 for Neolithic ($n = 155$). The differences in these values largely reflects sample size; their average dimorphism values vary only slightly (1.12, 1.13, and 1.11, respectively). The maximum dimorphism for the same measurement among the KRM fossils is 1.50 ($n = 3$); average dimorphism—calculated with KRM

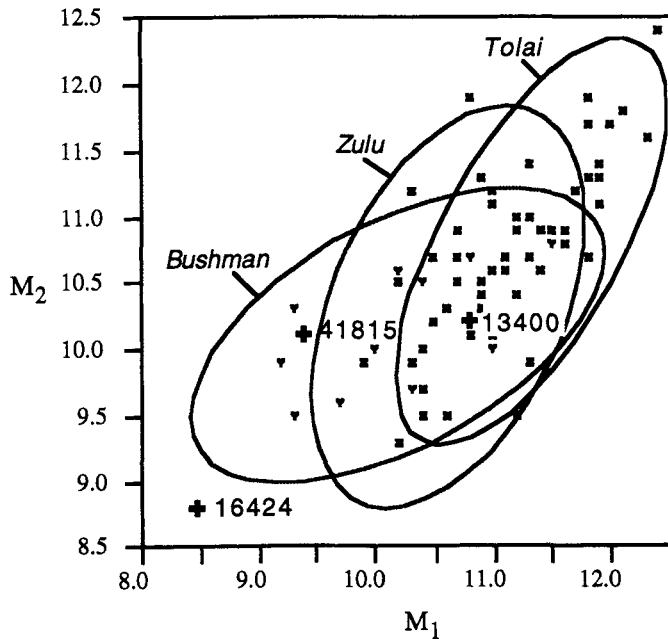


Fig. 5. Bivariate plot of molar dimensions (mm) for modern samples with 95% density ellipses. Tolai, Bushman, and Zulu individuals are represented, respectively, by "X," "Y," and "Z."

16424 as the only female—is slightly lower at 1.47. In comparison with the modern human data collected for the present study, the maximum dimorphism in the KRM sample exceeds that of the Bushmen for all measurements but that of the Tolai for only one: the diameter of M_1 . Again, this is a likely effect of the larger sample size for the Tolai. While the size difference between the two maxillae recovered from the LBS member (Bräuer et al., 1992) provides additional support for Rightmire and Deacon's (1991) observation of high sexual dimorphism among KRM hominids, a larger sample is required to determine how this population conforms to expected evolutionary trends.

It is unclear how closely sexual dimorphism in mandibles is correlated with that in other skeletal elements. In her study of the skull of indigenous South Africans, de Villiers (1968:201) noted that "sexual differentiation is most pronounced in the mandible, less so in the facial skeleton and least pronounced in the cranial vault." Similarly, Ox-

nard (1987:76) observed that in Neandertals and *Homo erectus*, "as with all extant forms examined so far, sexual dimorphism is considerably greater in the lower jaw than in the upper." It does not appear inappropriate to use the degree of sexual dimorphism in the jaw as a general proxy for sexual dimorphism in body size when making intraspecific comparisons, although it must be noted that this will likely result in a slight overestimate.

The mandible is considered by many osteologists to be potentially diagnostic of sex on morphological, as well as metric, grounds (Buikstra and Mielke, 1985; Enlow, 1990, and references therein), with the two most useful features being the chin and the gonial angle. Unfortunately, neither is preserved on KRM 16424. While the larger mandibular specimens preserve the symphysis, it is possible to estimate the gonial angle only on KRM 41815. Overall, the fragmentary nature of these fossils precludes any assessment of sexual dimorphism in mandibular morphology.

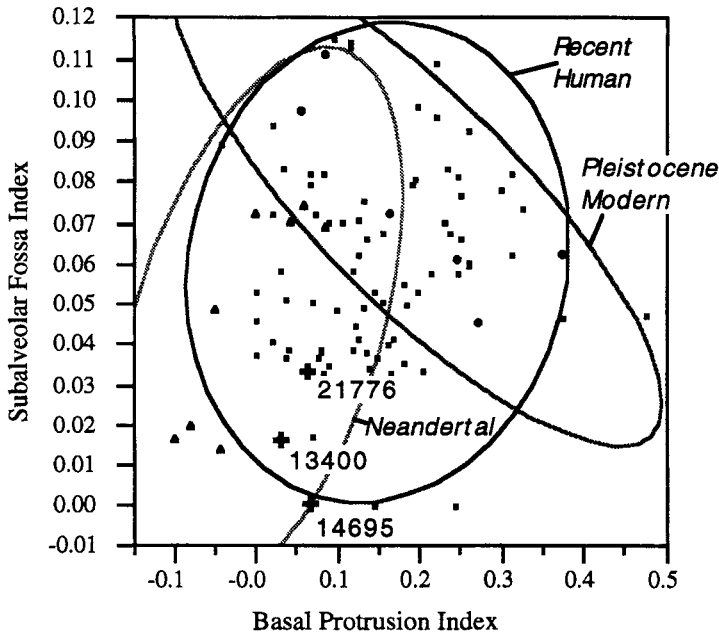


Fig. 6. Bivariate plot of chin indices for comparative samples with 95% density ellipses. Symbols as in Figure 4.

The occurrence of a hominid the size of KRM 16424 in the early Upper Pleistocene is not important simply for establishing an extreme degree of sexual dimorphism; its *absolute* size is also of diagnostic significance. The recovery of a similarly gracile maxillary specimen (Z44/SAS4SHC) from the lower LBS member (Bräuer et al., 1992) indicates that the occurrence of this extremely small mandible is not an anomaly. Most notably, it suggests that efforts to classify other KRM fossils as archaic on the basis of size were inappropriate in light of their emphasis on the larger fossils. If a reduction in facial and dental dimensions characterized the direction of human evolution in the Upper Pleistocene (Frayer 1980, 1984, 1992), then KRM 16424 provides equally—if not more—convincing evidence for the presence of modern humans than the arguably hyper-robust KRM 16651 zygomatic provides for the presence of archaic forms. The buccolingual diameters of the M_1 and M_2 of KRM 16424 measure 8.5 mm and 8.8 mm, respectively (Singer and Wymer, 1982). Wolpoff's (1971)

global survey of tooth size documented only a single M_1 as small as—and only a half-dozen M_2 specimens smaller than—that of this fossil. In addition, Bräuer and Mehlman (1988) documented a breadth of 9.2 mm for a 130,000-year-old M_2 from Mumba Rock Shelter, the smallest such measurement recorded for recent and prehistoric Tanzanians. The reduction in the size of human teeth between the Pleistocene and the Holocene has been attributed by some (Brace and Mahler, 1971; Calcagno, 1989) to the use of extraoral processing methods for food items, but there is no archaeological evidence of the practice of any such method during the early Upper Pleistocene. The presence of fossils of great antiquity with tiny teeth from both east and South Africa suggests that tooth size may have fluctuated widely during the course of recent human evolution.

The chin has been recognized as a synapomorphy of anatomically modern humans (Stringer et al., 1984; Stringer and Andrews, 1988), while its evolutionary significance has been the subject of continuing debate. Its

development corresponds with the reduction in mandibular length and/or the size of the anterior dentition that occur first and uniquely among hominids in anatomically modern humans (Daegling, 1993; Weidenreich, 1936). While the chin is believed to offer some mechanical advantage during mastication (Wolff, 1984), particularly in resisting the torsional forces resulting from asymmetrical loads (Enlow, 1990), it is unclear how much of its evolution—and the corresponding shortening of the jaw—is attributable to adaptations toward increased masticatory efficiency. Spencer and Demes (1993) have demonstrated that the longer jaw of Neandertals, despite being better designed for generating anterior bite forces, is not compromised in posterior bite potential. There is no evidence in the archaeological record to suggest that the appearance of the chin in the early Upper Pleistocene coincided with a shift in dietary and subsistence patterns.

Some insight into the chin problem may be gained by examining the evolution of this feature in the Neandertal lineage. Despite its identification as a synapomorphy of anatomically modern humans, this and previous studies have documented a common occurrence of incipient chins among Neandertals, particularly among the Vindija fossils (Ahren and Smith, 1993; Smith, 1982, 1984, 1994; Wolpoff, 1980; Wolpoff et al., 1981). Spencer and Demes (1993) found no significant difference in mandibular length between archaic *Homo sapiens* and Neandertals. However, a number of studies (Smith, 1984, 1993; Wolpoff, 1980) have observed a decrease in jaw size and an increase in chin development within the Neandertal lineage through time. These studies demonstrate that the terminal Middle Pleistocene Krapina sample displays a much less pronounced chin morphology than the later Neandertal specimens, particularly those from Vindija. A question that arises from these observations is whether the reduction in the length of the Neandertal jaw (its “long nonhuman mouth,” as described by Lieberman [1991]) and the corresponding appearance of its chin can be linked to glottogenesis (Robinson, 1914), which has been argued by some to be the critical synapomorphy distin-

guishing anatomically modern humans from their archaic predecessors and contemporaries (Milo and Quiatt, 1993). Overall, evidence exists to support the suggestion that the incipient chin morphology observed for a number of Neandertal fossils may not be homologous to that present in modern humans (Lieberman, 1995).

In the case of the KRM sample, chin development is obviously much less pronounced than would be expected in extant populations. Tillier (1989, 1990) has observed a similar situation among the early Upper Pleistocene hominids from Qafzeh, noting that the chin development of these early anatomically modern humans seemed retarded in comparison to modern Europeans. Each KRM mandible that cannot be aged on the basis of dentition appears too large to represent a juvenile, so Frayer et al.'s (1993) argument concerning the frontal fragment cannot be adopted to explain the poorly developed chins observed here. Hublin and Tillier (1981) have suggested that juvenile Neandertals often exhibit some, but not all, of the elements of a modern human chin. At the same time, they have documented the incipient presence of all such elements, including the tuber symphyseos, tubercula lateralia, and an incurvatio mandibulae anterior, on the mandible of the Jebel Irhoud 3, an 8–9-year-old juvenile dated by Grün and Stringer (1991) to isotope stage 5 or 6. Such observations of variability in the morphology of the mandibular symphysis raise the possibility that the chin is not a synapomorphy of anatomically modern humans, but rather a trait that evolved at variable rates and in different patterns in Africa, southwest Asia, and Europe during isotope stages 5–3 (Frayer, 1992; Hublin and Tiller, 1981; Smith, 1984; Tiller 1989, 1990; Wolpoff et al., 1981).

CONCLUSIONS

The disagreement over the phylogenetic attribution of the KRM mandibles partly reflects the lack of consensus concerning a systematic definition of anatomically modern humans. Attempts to define this taxon on the basis of explicit criteria (e.g., Day and Stringer, 1982; Kidder et al., 1993) have been

unable to delimit a range of morphological variability sufficient to include all modern humans and simultaneously exclude all individuals recognized as archaic. The study of modern human origins will benefit from current efforts to explain, rather than simply define, this wide range of variability (Lahr and Foley, 1994).

Despite their claim that the KRM hominid remains display archaic features, the opponents of the single recent origin hypothesis (e.g., Frayer et al., 1993, 1994; Smith, 1992, 1993; Wolpoff, 1992; Wolpoff and Caspari, 1990) have refrained from attributing these specimens to a specific taxon. In terms of chin development, the KRM specimens do not represent "mandibles of *sapiens* and Neanderthal type" (Wymer, 1982:139); their morphology falls directly between these two groups. The size of the larger specimens is not taxonomically diagnostic, falling well within the range of all comparative samples, but the extremely small size of KRM 16424 is notable for an early Upper Pleistocene hominid fossil and supports claims of modernity for the KRM sample.

The primitive morphology of the KRM mandibles is consistent with a wide range of different evolutionary interpretations: (1) It may reflect admixture between contemporary archaic and modern hominid groups, along the lines of that implied by Bräuer's (1992) Hybridization and Replacement Hypothesis or Smith's Assimilation Hypothesis (Smith et al., 1989) for non-African populations. (2) It may represent a transitional form between archaic and modern populations. Stringer and Bräuer (1994) recently expressed their agreement with Smith's (1992:148) assessment of the early Upper Pleistocene African fossils: "the somewhat primitive aspects of certain features in this sample (particularly in the KRM fossils), like brow ridge development and mandibular symphyseal morphology in some specimens, are to be expected in early representatives of modern humans and help to establish their phylogenetic connection to earlier, more archaic Africans." (3) It may simply reflect the high degree of intrapopulational variability documented for mandibular morphology among modern human populations. The presence of a specimen as small as KRM

16424 would seem least anomalous under this interpretation.

Compared with other Last Interglacial hominids, the KRM mandibles exhibit noticeably greater chin development than the Krapina Neandertals but less than those of the Skhul and Qafzeh fossils. Without a comparative sample of securely dated hominid mandibles representing adjacent time periods in African prehistory, the phylogenetic affinity of the KRM fossils remains equivocal.

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LITERATURE CITED

- Ahren JC, and Smith FH (1993) The transitional nature of the late Neanderthal mandibles from Vindija Cave, Croatia. *Am. J. Phys. Anthropol. Suppl.* 16:47.
- Armstrong GJ, and Van Gerven DP (1980) Sexual dimorphism and human evolution. *J. Hum. Evol.* 9:437-446.
- Brace CL, and Mahler PE (1971) Post-Pleistocene changes in the human dentition. *Am. J. Phys. Anthropol.* 34:191-204.
- Brace CL, and Ryan AS (1980) Sexual dimorphism and human tooth size differences. *J. Hum. Evol.* 9:417-435.
- Bräuer G (1988) Osteometrie. In R Knussmann (ed.): *Anthropologie: Handbuch der vergleichenden Biologie des Menschen. Band I: Wesen und Methoden der Anthropologie.* Stuttgart: Gustav Fischer Verlag, pp. 160-232.
- Bräuer G (1992) Africa's place in the evolution of *Homo*

- sapiens*. In G Bräuer and FH Smith (eds.): Continuity or Replacement: Controversies in *Homo sapiens* Evolution. Rotterdam: Balkema, pp. 83–98.
- Bräuer G, and Mehlman MJ (1988) Hominid molars from a Middle Stone Age level at the Mumba Rock Shelter, Tanzania. *Am. J. Phys. Anthropol.* 75: 69–76.
- Bräuer G, and Singer R (1996) The Klasies zygomatic bone: Archaic or modern? *J. Hum. Evol.*, 30:161–165.
- Bräuer G, Deacon HJ, and Zipfel F (1992) Comment on the new maxillary finds from Klasies River, South Africa. *J. Hum. Evol.* 23:419–422.
- Brown P (1989) Coobool Creek: A Morphological and Metrical Analysis of the Crania, Mandibles and Dentitions of a Prehistoric Australian Human Population. *Terra Australis* 13. Canberra: Department of Prehistory, Australian National University.
- Brown P (1993) Recent human evolution in East Asia and Australasia. In MJ Aitken, CB Stringer, and PA Mellars (eds.): The Origin of Modern Humans and the Impact of Chronometric Dating. Princeton: Princeton University Press, pp. 217–233.
- Buikstra JE, and Mielke JH (1985) Demography, diet, and health. In RI Gilbert and JH Mielke (eds.): The Analysis of Prehistoric Diets. Orlando: Academic Press, pp. 359–422.
- Calcagno JM (1989) Mechanisms of Human Dental Reduction: A Case Study from Post-Pleistocene Nubia. Lawrence, KS: University of Kansas Publications in Anthropology.
- Daegling DJ (1993) Functional morphology of the human chin. *Evol. Anthropol.* 1:170–176.
- Day MH, and Stringer CB (1982) A reconsideration of the Omo Kibish remains and the *erectus-sapiens* transition. In M de Lumley (ed.): *L'Homo erectus et la Place de l'Homme de Tautavel Parmi les Hominides Fossiles*. Nice: Louis-Jean Scientific and Literary Publications, pp. 814–846.
- de Villiers H (1968) The Skull of the South African Negro. Johannesburg: Witwatersrand University Press.
- Deacon HJ (1993) Southern Africa and modern human origins. In MJ Aitken, CB Stringer, and PA Mellars (eds.): The Origin of Modern Humans and the Impact of Chronometric Dating. Princeton: Princeton University Press, pp. 104–117.
- Deacon HJ, and Geleijnse VB (1988) The stratigraphy and sedimentology of the main site sequence, Klasies River, South Africa. *S. Afr. Arch. Bull.* 43:5–14.
- Deacon HJ, and Shuurman R (1992) The origins of modern people: The evidence from Klasies River. In G Bräuer and FH Smith (eds.): Continuity or Replacement: Controversies in *Homo sapiens* Evolution. Rotterdam: A.A. Balkema, pp. 121–130.
- Enlow DH (1990) Facial Growth. Philadelphia: W.B. Saunders.
- Frayser DW (1980) Sexual dimorphism and cultural evolution in the Late Pleistocene and Holocene of Europe. *J. Hum. Evol.* 9:399–415.
- Frayser DW (1984) Biological and cultural changes in the European Late Pleistocene and Early Holocene. In FH Smith and F Spencer (eds.): The Origins of Modern Humans: A World Survey of the Fossil Evidence. New York: Alan R. Liss, pp. 211–250.
- Frayser DW (1992) Evolution at the European edge: Neanderthal and Upper Paleolithic relationships. *Préhistoire Européenne* 2:9–69.
- Frayser DW, and Wolpoff MH (1985) Sexual dimorphism. *Annu. Rev. Anthropol.* 14:429–473.
- Frayser DW, and Wolpoff MH (1993) Comment on Milo RG, and Quiatt D, "Glottogenesis and anatomically modern *Homo sapiens*." *Curr. Anthropol.* 34:582–584.
- Frayser DW, Wolpoff MH, Thorne AG, Smith FH, and Pope GG (1993) Theories of modern human origins: The paleontological test. *Am. Anthropol.* 95:14–50.
- Frayser DW, Wolpoff MH, Thorne AG, Smith FH, and Pope GG (1994) Getting it straight. *Am. Anthropol.* 96:424–438.
- Grün R, and Stringer CB (1991) Electron spin resonance dating and the evolution of modern humans. *Archaeometr.* 33:153–199.
- Howells WW (1989) Skull Shapes and the Map: Craniometric Analysis of Modern *Homo*. Cambridge: Harvard University Press.
- Hublin JJ, and Tillier AM (1981) The Mousterian juvenile mandible from Irhoud (Morocco): A phylogenetic interpretation. In CB Stringer (ed.): Aspects of Human Evolution. London: Taylor and Francis, pp. 167–185.
- Kennedy KAR (1984) Biological adaptations and affinities of Mesolithic South Asians. In JR Lukacs (ed.), The People of South Asia: The Biological Anthropology of India, Pakistan, and Nepal. New York: Plenum, pp. 29–57.
- Kidder JH, Jantz RL, and Smith FH (1992) Defining modern humans: a multivariate approach. In G Bräuer and FH Smith (eds.): Continuity or Replacement: Controversies in *Homo sapiens* Evolution. Rotterdam: Balkema, pp. 157–177.
- Lahr MM, and Foley R (1994) Multiple dispersals and modern human origins. *Evol. Anthropol.* 3:48–60.
- Lieberman DE (1995) Testing hypotheses about recent human evolution from skulls. *Curr. Anthropol.* 36: 159–197.
- Lieberman P (1991) Uniquely Human. Cambridge: Harvard University Press.
- Milo RG, and Quiatt D (1993) Glottogenesis and anatomically modern *Homo sapiens*. *Curr. Anthropol.* 34: 569–598.
- Oxnard CE (1987) Fossils, Teeth and Sex. Seattle: University of Washington Press.
- Rightmire GP (1975) Problems in the study of Later Pleistocene man in Africa. *Am. Anthropol.* 77:28–52.
- Rightmire GP (1981) Later Pleistocene hominids of eastern and southern Africa. *Anthropologie (Brno)* 19: 15–26.
- Rightmire GP (1986) Africa and the origins of modern humans. In R Singer and JK Lundy (eds.): Variation, Culture and Evolution in African Populations. Johannesburg: Witwatersrand University Press, pp. 209–220.
- Rightmire GP, and Deacon HJ (1991) Comparative studies of Late Pleistocene human remains from Klasies River Mouth, South Africa. *J. Hum. Evol.* 20:131–156.
- Rink WJ, Schwarcz HP, Smith FH, and Radovic J (1995) ESR ages for Krapina hominids. *Nature* 378:24.
- Robinson L (1914) The story of the chin. *Annu. Rep. Smithsonian Inst.* 1914:599–610.
- Singer R, and Wymer J (1982) The Middle Stone Age at

- Klasies River Mouth in South Africa. Chicago: University of Chicago Press.
- Smith FH (1982) Upper Pleistocene hominid evolution in south-central Europe: A review of the evidence and analysis of trends. *Curr. Anthropol.* 23:667–703.
- Smith FH (1984) Fossil hominids from the Upper Pleistocene of central Europe and the origin of modern Europeans. In FH Smith and F Spencer (eds.): *The Origins of Modern Humans: A World Survey of the Fossil Evidence*. New York: Alan R. Liss, pp. 137–209.
- Smith FH (1992) The role of continuity in modern human origins. In G Bräuer and FH Smith (eds.): *Continuity or Replacement: Controversies in *Homo sapiens* Evolution*. Rotterdam: Balkema, pp. 145–156.
- Smith FH (1993) Models and realities in modern human origins: The African fossil evidence. In MJ Aitken, CB Stringer, and PA Mellars (eds.): *The Origin of Modern Humans and the Impact of Chronometric Dating*. Princeton: Princeton University Press, pp. 234–248.
- Smith FH (1994) Samples, species, and speculations in the study of modern human origins. In MH Nitecki and DV Nitecki (eds.): *Origins of Anatomically Modern Humans*. New York: Plenum, pp. 227–249.
- Smith FH, Falsetti AB, and Donnelly S (1989) Modern human origins. *Yearb. Phys. Anthropol.* 32:35–68.
- Spencer MA, and Demes B (1993) Biomechanical analysis of masticatory system configuration in Neanderthals and Inuits. *Am. J. Phys. Anthropol.* 91:1–20.
- Stringer CB, and Andrews P (1988) Genetic and fossil evidence for the origin of modern humans. *Science* 239:1263–1268.
- Stringer CB, and Bräuer G (1994) Methods, misreading, and bias. *Am. Anthropol.* 96:416–424.
- Stringer CB, Hublin JJ, and Vandermeersch B (1984) The origin of anatomically modern humans in Western Europe. In FH Smith and F Spencer (eds.): *The Origins of Modern Humans: A World Survey of the Fossil Evidence*. New York: Alan R. Liss, pp. 51–135.
- Stringer CB, Grün R, Schwarcz H, and Goldberg P (1989) ESR dates for the hominid burial site of Es Skhul in Israel. *Nature* 338:756–758.
- Tillier AM (1981) Evolution de la région symphysaire chez les *Homo sapiens* juveniles du Paléolithique moyen: Pech de l'Aze 1, Roc de Marsal et La Chaise 13. *C. R. Acad. Sci. Ser. III* 293:493–495.
- Tillier AM (1989) The evolution of modern humans: Evidence from young Mousterian individuals. In P Mellars and CB Stringer (eds.): *The Human Revolution*. Princeton, NJ: Edinburgh University Press, pp. 286–297.
- Tillier AM (1990) Mandibular growth and tooth size in Qafzeh early modern humans. *Am. J. Phys. Anthropol.* 81:307.
- Valladas H, Reyss JL, Joron JL, Valladas G, Bar-Yosef O, and Vandermeersch B (1988) Thermoluminescence dating of the Mousterian proto-Cro-Magnon remains of Qafzeh Cave (Israel). *Nature* 331:614–616.
- Weidenreich F (1936) The mandibles of *Sinanthropus pekingensis*: A comparative study. *Palaeontologia Sinica*, Series D, Volume 7(3).
- Wolff JEA (1984) A theoretical approach to solve the chin problem. In DJ Chivers, BA Wood, and A Bilsborough (eds.): *Food Acquisition and Processing in Primates*. New York: Plenum Press, pp. 391–405.
- Wolpoff MH (1971) *Metric Trends in Hominid Dental Evolution*. Cleveland: Case Western Reserve University Press.
- Wolpoff MH (1980) *Paleoanthropology*. New York: Alfred A. Knopf.
- Wolpoff MH (1992) Theories of modern human origins. In G Bräuer and FH Smith (eds.): *Continuity or Replacement: Controversies in *Homo sapiens* Evolution*. Rotterdam: A.A. Balkema, pp. 25–54.
- Wolpoff MH, and Caspari R (1990) On Middle Paleolithic/Middle Stone Age hominid taxonomy. *Curr. Anthropol.* 31:394–395.
- Wolpoff MH, Smith FH, Malez M, Radovcic J, and Rukavina D (1981) Upper Pleistocene human remains from Vindija Cave, Croatia, Yugoslavia. *Am. J. Phys. Anthropol.* 54:499–545.
- Wymer J (1982) *The Palaeolithic Age*. New York: St. Martin's Press.